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The Density, Distribution, and Activity Patterns of Woodchucks in Cades Cove, Great Smoky Mountains National Park

Cathy A. Taylor
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To the Graduate Council:

I am submitting herewith a thesis written by Cathy A. Taylor entitled "The Density, Distribution, and Activity Patterns of Woodchucks in Cades Cove, Great Smoky Mountains National Park." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology and Evolutionary Biology.

Michael R. Pelton, Major Professor

We have read this thesis and recommend its acceptance:

James T. Tanner, A. C. Echternacht

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Accepted for the Council:

Vice Chancellor
Graduate Studies and Research

THE DENSITY, DISTRIBUTION, AND ACTIVITY PATTERNS OF WOODCHUCKS IN CADES COVE, GREAT SMOKY MOUNTAINS NATIONAL PARK

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Cathy A. Taylor

June 1979

DEDICATION

I dedicate this thesis to my parents, Richard and Betty Taylor, who wholeheartedly supported me through many years of study; to friends who supported me when the completion of this thesis seemed forever beyond my grasp; and to the early settlers of Cades Cove and the southern Appalachians and particularly to those who sang this song:

Oh, Groundhog--Anonymous

Wake up Granddaddy, get your dog,
Wake up Granddaddy, get your dog,
Goin' up the hollar to catch a groundhog,
Oh, groundhog.

Whistle up your dog and shoulder up your gun,
Whistle up your dog and shoulder up your gun,
Got that groundhog on the run,
Oh, groundhog.

Yonder comes Billy with a 10 foot pole,
Yonder comes Billy with a 10 foot pole,
Twist that groundhog right out of his hole,
Oh, groundhog.

I dug down but I didn't dig deep,
I dug down but I didn't dig deep,
Caught that groundhog fast asleep,
Oh, groundhog.

Yonder comes Sally with a snicker and a grin,
Yonder comes Sally with a snicker and a grin,
Whistle-pig grease all over her chin,
Oh, groundhog.

Eat the meat and tan the hide,
Eat the meat and tan the hide,
Makes the best shoe lace ever was tied,
Oh, groundhog.

Look out boys I'm 'bout to fall,
Look out boys I'm 'bout to fall,
Eat 'til my britches won't button at all,
Oh, groundhog.

Little piece of meat sittin' on the shelf,
Little piece of meat sittin' on the shelf,
If you want any more better get it yourself,
Oh, groundhog.

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ABSTRACT

The purpose of this study was to delineate certain population characteristics and behavioral aspects of the woodchuck (Marmota monax) in the southeastern extremity of its range. Random quadrats from a grid system of the Cades Cove area, GSMNP, were systematically searched for active woodchuck burrow systems during the summers of 1976, 1977, and 1978. All burrow systems, topographical features, and buildings were marked on a scaled drawing and various burrow dimensions and land usage were recorded. Twice weekly between 7 July 1977 and 11 July 1978, observations were made of woodchucks to assess behavioral responses to the environment.

Seventy-five percent of active burrows were found to house permanent residents resulting in population estimates of 814, 1735, and 1351 woodchucks in Cades Cove for 1976, 1977, and 1978, respectively. The population was aggregated in response to land use and the availability of cover. Competition with cattle, predation and social interactions apparently influenced population numbers.

Mean activity observed per hour changed throughout the year in response to changing densities of non-hibernating woodchucks and changing activity levels per individual. Mean activity of woodchucks in Cades

Cove differed from more northern populations due to a longer growing season and a shorter period of hibernation. Frequency distributions of various behaviors changed with season and time of day in response to reproductive condition, environmental conditions, and social interactions. Foraging was predominant during all seasons though it occurred less frequently than in northern populations. Alert positions occurred more frequently in summer and fall than during winter and spring. Resting, alert, traveling, and social behaviors were more prevalent during the morning while foraging was the dominant behavior during the afternoon. Daily activity patterns changed throughout the year with a unimodal distribution occurring in spring and fall and a bimodal distribution occurring in late spring and summer. The bimodal pattern was not found to occur in response to temperature as suggested by earlier researchers but rather was thought to be a result of individual activity levels. Cloud cover, temperature, and precipitation were found to affect activity over a yearly period, though differences were found in the seasonal effects of those variables. Though not significant over a year, relative humidity influenced behavior during certain seasons.

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INTRODUCTION

Originally a forest dweller, the woodchuck has readily adapted to the open fields and meadows created by agriculture and civilization. Schoonmaker (1966) attributes this conversion to greater accessibility of food and increased light intensity. Optimum habitat for the woodchuck has been described as woods' edge and brushy fence rows (de Vos and Gillespie 1960, Schoonmaker 1966) as well as open fields of soybeans, hay and alfalfa (Grizzell 1955, Schoonmaker 1966). However, open woods and brushy or rocky ravines have also been cited as den and foraging sites (Howell 1915, Caras 1967, Burt and Grossenheider 1976). In recent years, interstate medians, orchards, and abandoned cemeteries have become common burrowing sites (Schoonmaker 1966, Doucet et al. 1974). Merriam (1971) asserts that vegetation has little effect on burrow location, however Merriam and Merriam (1965) and Thompson (1971) have demonstrated a strong influence by burrows on the immediate vegetation due to the alteration of soil nutrients and moisture and to the effects of foraging.

Soil texture and drainage classes have also been shown to affect burrow location. Sandy loams, fine sandy loams, and silt loams which are well-drained have been shown to be preferred burrowing sites (Moss 1940, Currier

1949, Anthony 1962, Merriam 1971). Some authors listed steep slopes as preferable (Merriam 1971, Henderson and Gilbert 1978) while others regarded gradual slopes and flat areas as ideal (Twichell 1939, Grizzel 1955). Two types of burrows are apparently utilized; a summer burrow, characterized by open areas on flat or gently rolling topography, and a hibernation den, which is usually found in wooded or brushy habitat (Hamilton 1934, Twichell 1939, Grizzell 1955, Schoonmaker 1966).

Woodchucks must spend the summer months building up fat stores to carry them through winter hibernation. These stores are utilized for several weeks following emergence from hibernation since vegetation is sparse and woodchucks are intent on mating (Snyder and Christian 1960, Davis 1967a). In relation to this behavior, Snyder et al. (1961) and Bailey (1965a) describe a six-month period of weight gain counteracted by a six-month period of weight loss. Fall (1971), however, found indications of a rhythm slightly less than one year, a factor that explains differences in hibernation for different age classes. These studies seem to suggest a circannual rhythm, as well as a seasonal change in foraging behavior (Davis and Finnie 1975).

Although much recent research on Marmota monax has dealt with the physiological aspects of hibernation, other areas of its life history are being pursued. Behavioral

aspects of the woodchuck have received considerable attention. Bronson (1963, 1964) found that aggressive encounters decrease steadily following the reproductive period, possibly caused by a drop in androgen levels as indicated by a weight change of the seminal vesicles. A subsequent increase in such encounters around July was correlated with a large increase in population due to the dispersal of young. A study of mother-infant relations indicates that increased aggression shown by the female towards her young prior to their dispersal contributes to the high agonistic behavior levels seen at that time (Barash 1974a).

Barash (1974b) correlates the relative aggressiveness of the woodchucks with their solitary lifestyle, an existence permitted by the relatively long growing season that occurs within its range. The harsher environments inhabited by other marmots require colonial living and less aggressive interaction among members of the colony. The aggressiveness of the woodchuck appears to be seasonally influenced rather than density influenced (Bronson 1963, Armitage 1975, 1977), although aggressive interactions were lower in high density populations than in low density populations. Population density was important in determining the rate of contact, but season determined the animals' reactions to that contact.

Other behavioral work has centered on both seasonal

and daily activity patterns. Bronson (1962) found that daily activity levels of woodchucks in Pennsylvania increased from the time of emergence from hibernation until after the young dispersed, then decreased until the cessation of activity due to hibernation. Changes in daily activity patterns were also demonstrated with a unimodal distribution characterizing activity from February through April and from September to November and a bimodal distribution occurring from May through August. This bimodal pattern was also found by ethological studies in New York (Conrad and Fidura 1970) and telemetric work in Arkansas (Hayes 1976). The latter study contradicted earlier telemetric work by Merriam (1966) in which increases in midday interburrow movements appeared to offset a bimodal distribution of activity. Hayes (1976) suggested that bimodal patterns are caused by the inhibition of activity at temperatures above 31° C. Further study is required to substantiate this claim and to delineate the influences of environmental factors on woodchuck activity.

The majority of the studies on woodchuck populations have taken place in New York, Pennsylvania, Canada, and Maryland. The range of the woodchuck, however, extends from that region westward to the Pacific Coast through southern Canada, and southward through the southeastern United States to Alabama, Tennessee, and Arkansas (Burt

and Grossenheider 1976). In order to evaluate the effects of environmental factors on woodchuck activity, studies must also be carried out in the extremities of its range.

The Cades Cove area of the Great Smoky Mountains National Park (GSMNP) provides an ideal setting for a study of Marmota monax in the Southeast. Situated within the Park, the area is maintained in hay production and cattle grazing, providing 976.9 ha of prime habitat for the woodchuck, as well as eliminating hunting pressures. The population can be directly compared to other populations on farmlands in the Southeast that are continually exploited. This information is necessary in order to develop management plans for the species and to establish baseline data for the future monitoring of woodchuck populations.

In a preliminary study, an undergraduate researcher estimated the 1976 population of woodchucks in Cades Cove to be 814 (Brooks 1976). This animal is a popular attraction for park visitors and appears to be a major prey for resident predators. Their burrows provide dens for other animals that inhabit the Cove, including red and gray fox (Vulpes vulpes, Urocyon cinereoargenteus), cottontail rabbits (Sylvilagus floridanus), skunks (Mephitis mephitis), and raccoons (Procyon lotor). Leasees, rangers, and park visitors have remarked on the increase of woodchucks in Cades Cove during the past several years. In order to assess the state of the population, yearly estimates are required.

With these considerations in mind, the primary objectives of this project were to estimate the population densities of woodchucks for the summers of 1976, 1977, and 1978, to evaluate trends in population numbers and distributions, and to assess daily and seasonal activity patterns in relation to environmental factors. An additional objective was to evaluate frequency distributions of behaviors exhibited daily and seasonally with regard to environmental influences.

CHAPTER I

STUDY AREA

Cades Cove is found within Blount County, Tennessee, in the Great Smoky Mountains National Park (Figure 1). This gently rolling, open area is surrounded by densely forested mountains. The evenness of the Cove floor made it ideal for settlement in the 1800's and due to this historical heritage, the Cove is presently maintained by the park as an exhibition depicting the cultural aspects of early pioneer life. The Cove itself is, however, no longer broken up into the small farm plots reminiscent of the period. Of the 976.9 ha that comprise the Cove, 76.5% (747.3 ha) are open areas maintained by cattle grazing and haying operations carried out by three permittee operations under National Park Service supervision. Approximately 500 cattle and 40 horses are pastured in the area. The remaining 23.5% (229.6 ha) is covered with small woodlots.

A one-way, single-laned, paved road, known as the Cades Cove Loop Road, circles the 17.6 km perimeter of the study area (Figure 1). Two gravelled roads transect the Cove, allowing access to barns, storage areas, and pastures. Gates to all roads are closed from sundown until 0600 hr and all visitor traffic is excluded during those hours.

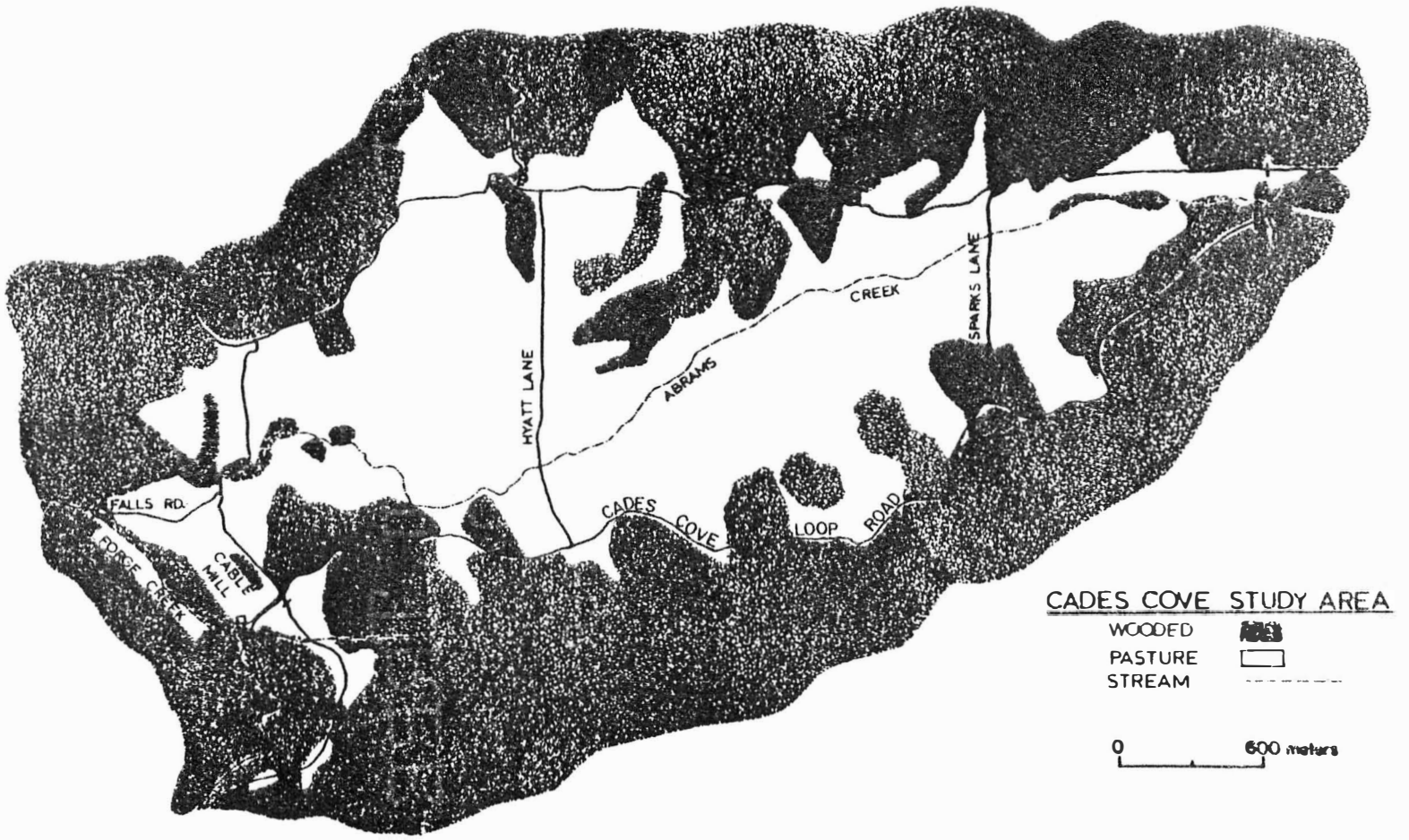

Figure 1. Cades Cove in the GSMNP.

The Cove lies at 35° N. latitude and 83° W. longitude, with elevation ranging from 518 to 599 m. Abrams Creek and its tributaries constitute 36.8 km of streams that drain the Cove. Many of the smaller branches dry up during the summer and portions of Abrams Creek may occasionally be dry during July and August. Several small swampy areas occur along the creek.

Vegetation within the pastures consists primarily of grasses and clovers. Fescue (Festuca sp.), orchard-grass (Dactylis sp.), timothy (Phleum sp.) and red and ladino clovers (Trifolium sp.) are the dominant groups found in hayfields. In addition, Solanum carolinense is common in the pastures and willow grass (Microstegium sp.) and smart weed (Polygonum sp.) dominate the edges of woodlots and creekbanks.

Many woodlots within the Cove contain nearly pure stands of white pine (Pinus strobus) and shortleaf pine (P. echinata) while the understory often contains hemlock (Tsuga canadensis). Mixed deciduous woodlots are also common, containing tulip poplar (Liriodendron tulipifera) and various species of oak (Quercus), maple (Acer), and hickory (Carya).

Cades Cove provides habitat for a diversity of wildlife species. The protected environment found within the park encourages a semi-tame nature in many species which allows high observability to visitors and researchers

alike. Some major species include black bear (*Ursus americanus*), white-tailed deer (*Odocoileus virginianus*), European wild hog (*Sus scrofa*), gray and red fox, gray squirrel (*Sciurus carolinensis*), raccoon, woodchuck, wild turkey (*Maleagris gallopavo*), ruffed grouse (*Bonasa umbellus*), and many passerine species such as the eastern bluebird (*Sialia sialis*).

CHAPTER II

METHODS AND MATERIALS

Density and Distribution

Density determination. A survey of the population density of woodchucks in Cades Cove, GSMNP, was conducted during the summers of 1976, 1977, and 1978. The original assumption underlying the 1976 study by Brooks (1976) was that a ratio of one woodchuck per burrow existed in the Cove. To test this assumption, diurnal observations were made during the summer of 1978. Binoculars (10 x 50 mm) and a 60 x spotting scope were used to determine the number of woodchucks utilizing individual burrow systems and the percentage of active burrows being used by permanent residents. These observations took place in areas mapped as to the number and location of burrows and were undertaken during peak activity in the summer (1700-2100 hr) in order to optimize observation time. The number of woodchucks and their movements were recorded and compared with the number of burrow systems. Twelve plots were observed and classified into the following habitat types: brushy areas, woodlots, hayfields, and pasture. Wooded areas were difficult to observe in this manner, although all sightings in wooded and other areas were recorded during the density study.

The sampling technique used in the surveys of population density of the woodchucks in Cades Cove incorporated the use of a 7.5 minute USGS quadrangle, topographical map. Brooks (1976) set up a 1 x 1 cm grid system labeled on an X,Y axis (Figure 2), which divided the Cove into plots measuring 244 x 244 m. Quadrats were randomly chosen from the map each summer, deleting those that fell 50% or more outside of the study area. Thirty-four plots, representing 20% of the area, were chosen for the summers of 1977 and 1978, though only 33 were chosen during the summer of 1976 (Brooks 1976).

The plots were located individually in the field by computing distances from topographical features and permanent structures. With the aid of a compass, the quadrats were paced off and the corners were marked with visible white stakes. Each plot was then systematically searched for burrow systems, with freshly excavated dirt, trails in the vegetation, and feces near the entrances indicating active burrows. All burrow systems, topographical features, buildings, and other landmarks were located on a scaled drawing. Various burrow dimensions were recorded for each active burrow system, dimensions varying according to year. The number of entrances, as well as distances to the nearest active burrow, nearest inactive burrow, water sources, and the road were recorded during all three years of the study. In addition, the

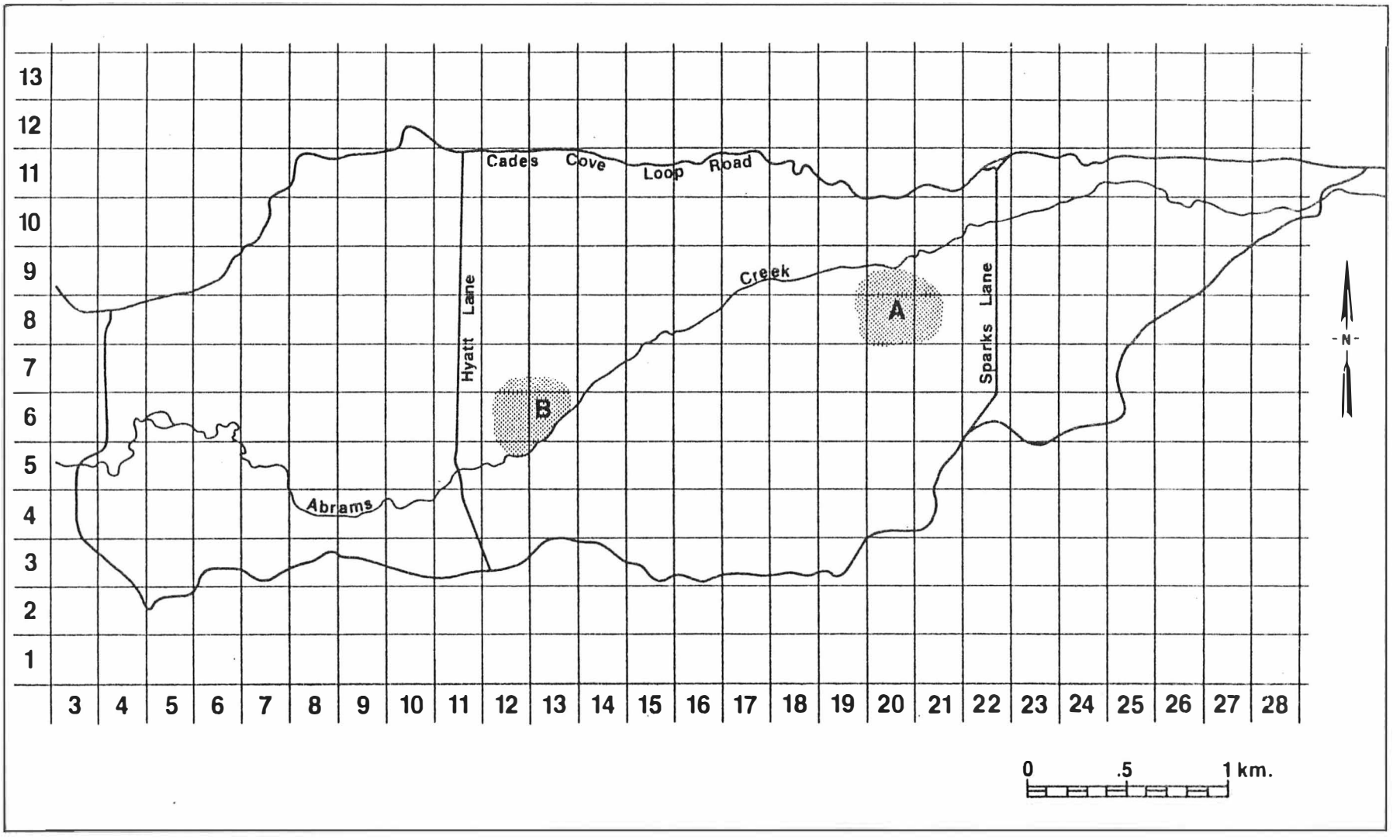

Figure 2. Grid system and observation areas in Cades Cove, GSMNP. Areas A and B were used for behavioral observations.

number of regular entrances and the number of plunge entrances were recorded for 1977 and 1978, while mound height and diameter and entrance diameter were measured in 1976 and 1977. The location of each burrow system was classified according to the following classification scheme: (1) hayfield, (2) pasture, (3) woodlot, less than 20 m to the edge, (4) woodlot, greater than 20 m to the edge, (5) brushy area, or (6) under a building.

Statistical analysis. Total population estimates were derived for each year by multiplying the average number of burrows per sampled quadrat by the total number of quadrats (162), then dividing by the sampling fraction and multiplying by 75% utilization (Tanner 1978). The sampling fraction was 20% of the Cove area. Population densities were calculated for each year as well as densities for the major habitat types (hayfield, pasture, and woodlot). Due to the non-normal distributions of the burrow systems, the Mann-Whitney U-test was used to compare population estimates between years. Burrow dimensions were analyzed between consecutive years with the use of a t-test. Where variances were unequal, Satterwaite's approximation was used to compute the degrees of freedom associated with the t approximation (Steel and Torrie 1960). Duncan's Multiple Range test was used to test for differences in burrow dimensions among habitat types with significance reported when $p < 0.05$.

The 34 quadrat maps from each of the three surveys were super-imposed on a soil survey map of Cades Cove (Elder et al. 1959). Burrow sites were located on the map and the soil texture and drainage classes were recorded.

Behavioral Analysis

Observations. Two areas in Cades Cove, GSMNP, were chosen to determine activity patterns of woodchucks and the effects of environmental variables on these patterns. These areas were chosen on the basis of optimal habitat, large population size, limited interference by park visitors and grazing animals, and the availability of observation points (Figure 2).

Observations began 7 July 1977 and continued until 11 July 1978. One day a week was allotted to each area with observations beginning shortly after sunrise and continuing until activity ceased; this was usually within one-half hour of sunset. From 6 December through 11 February, observations were shortened to two-three hours a week per field due to the decline in activity due to hibernation.

Each day of observation was divided into 10-minute intervals and a scan survey of the area was conducted during each period. Binoculars (10 x 50 mm) and a 60 x spotting scope were used to locate all woodchucks above

ground. The behavior of each subject when initially sighted during each scan observation was recorded as one of the following behavioral categories:

a. up-alert: animal sitting up with head erect and ears perked up;

b. down-alert: animal on all four feet, usually motionless, head up and ears perked;

c. foraging: animal on all four feet, feeding;

d. resting: animal lying down, head on ground or forelegs;

e. traveling: an animal moving between two burrow systems;

f. burrow maintenance: animal active at entrance, cleaning away debris; also the collection of dry grass and entrance into the burrow;

g. grooming: one animal cleaning self;

h. social interaction: animals facing each other, noses or faces in close proximity;

i. agonistic: animal in a threat posture, back arched, hair on back erect, head oriented toward opponent, mouth open; or actual fighting.

This list of behaviors was modified from a similar list compiled by Conrad and Fidura (1970). The last four categories were later combined into a single category due to their rare occurrences.

In addition, environmental variables were recorded

at one-half hour intervals and included ambient temperature, relative humidity, percentage cloud cover, and precipitation. Temperature and relative humidity were recorded to the nearest degree or percentage, respectively, while cloud cover was estimated to the nearest 10%. Precipitation fell into the following six categories: 0--no precipitation, 1--light rain or drizzle, 2--moderate rainfall, 3--heavy rainfall, 4--snow, and 5--sleet. Unnatural disturbances, such as tractors, people, dogs, and cattle were also noted.

Statistical analysis. Differences in behavioral frequencies were tested for the hypothesis of homogeneity between seasons and between consecutive months using a Chi Square contingency table ($p < 0.05$). In addition, the frequency distribution of behaviors that occurred in the morning (0600-1300 hrs) was compared with that of the afternoon (1300-2100 hrs). Similarly, daily activity patterns were grouped by season and by month and the hypothesis of homogeneity of activity patterns was tested in the same manner.

The hypothesis that time of year, time of day, and climatic factors had no effect on woodchuck activity was evaluated using least square analysis of variance procedures. In an attempt to clarify relationships among the independent variables, sequential sums of squares and partial sums of squares were analyzed simultaneously.

Since the sequential relationships can be affected by order of inclusion of the variables in the model, a strategy based on ease of measurement was chosen. The least squares analysis of variance procedures were run for individual seasons as well as for a one-year period. Direct and inverse relationships between climatic variables and activity were indicated by the least squares analysis of variance but were calculated by holding all other variables constant. These relationships were evaluated in conjunction with the biology of woodchucks and were reported when they seemed biologically consistent.

CHAPTER III

RESULTS AND DISCUSSION

I. DENSITY AND DISTRIBUTION

Animal Observations

One hundred and fifty-four active burrow systems were observed in 12 mapped areas. Of these, 115 burrow systems were found to contain a single resident woodchuck, resulting in a 75% rate of utilization. The remaining 39 systems were apparently auxillary burrows used for refuges during foraging and traveling. This estimate may be slightly lower than the actual figure due to the difficulty of observing woodchucks in brushy and wooded areas. Records of woodchucks observed in woodlots during the survey of quadrats supports the 75% residence figure. Grizzell (1955) also found that 75% of the active burrows in his study area in Maryland actually contained an animal.

Densities and Distributions

The original survey by Brooks (1976) indicated an average of 6.61 active woodchuck burrows per quadrat (Table 1) for a population estimate of 814 animals for the Cades Cove area and a density of 0.83 animals per ha. This procedure was repeated during the 1977 season and an average of 14.09 active burrows per plot resulted in

Table 1. Number of burrow systems for each quadrat surveyed in Cades Cove, identified by location (see Figure 2, page 13).

1976			1977			1978		
Plot Number	Total Burrows	Active Burrows	Plot Number	Total Burrows	Active Burrows	Plot Number	Total Burrows	Active Burrows
6, 4	3	3	5, 2	11	8	6,13	4	4
7, 4	11	11	2, 3	6	6	7,13	13	13
7, 5	11	11	7, 4	16	16	5, 5	7	7
7, 6	7	7	6, 5	8	6	3, 7	2	0
7, 7	7	7	4, 6	15	12	6, 8	14	14
4, 9	5	5	6, 6	14	14	11, 8	9	9
6, 9	8	8	7, 6	13	13	4, 9	15	10
9, 9	11	11	4, 8	27	16	5, 9	8	8
4,10	10	8	11, 8	12	12	6, 9	7	7
8,10	5	5	6, 9	7	7	9, 9	12	12
10,10	5	4	7, 9	16	16	11, 9	11	11
4,12	0	0	9, 9	21	21	11,10	6	5
12,12	2	2	7,10	5	5	3,12	3	2
6,14	6	5	10,10	12	10	5,12	17	15
5,15	13	9	5,12	17	15	6,12	11	11
6,15	6	6	8,12	18	14	8,12	18	15
5,16	19	16	11,13	6	6	6,13	21	21
11,17	5	4	6,14	15	13	6,14	9	7
5,18	8	8	7,15	12	11	9,14	8	6
6,18	5	5	3,16	9	6	3,15	2	2
7,19	6	5	5,16	22	22	4,15	23	22
7,20	2	2	9,17	19	15	8,15	10	9
10,20	10	10	11,17	13	12	5,16	32	32
6,21	2	2	4,18	30	30	10,16	5	3
10,22	9	9	8,18	19	19	10,17	12	9
6,23	6	6	4,19	20	18	6,18	5	5
7,23	4	3	6,19	12	6	8,19	26	26
9,23	7	7	10,20	15	15	4,20	7	7
11,23	10	10	8,21	30	30	8,21	21	21
6,24	10	10	7,22	37	31	7,23	3	3
9,24	9	9	10,23	20	17	11,23	18	18
9,25	2	2	8,25	16	12	8,24	10	8
10,25	8	8	9,25	16	16	10,24	19	17
			9,26	9	9	10,26	15	14
		218			479			373
		$\bar{X}$ = 6.61			$\bar{X}$ = 14.09			$\bar{X}$ = 10.97

an estimate of 1735 woodchucks (1.78/ha). These estimates indicate a 113% increase in the population size over a period of one year. A third estimate carried out during the 1978 summer season showed a 22% decrease in the population. An average of 10.97 burrows per plot gave an estimated 1351 woodchucks (1.38/ha) for the entire Cove (Table 1).

Ten identical plots were surveyed during 1976 and 1977 and eight identical plots during 1977 and 1978 (Tables 2 and 3). Although the population estimate for 1977 exhibited a 113% increase over 1976, only an 86% population increase occurred on the 10 duplicate plots. However, figures for individual plots revealed that increases much greater than 86% occurred in those fields that changed in usage from pasture to hay. Plot 9,25 revealed a 700% increase, plot 10,10 a 150% increase, and plot 6,14 a 160% increase in population after part or all of the area was converted to hay production.

A similar trend occurred during the 1977 and 1978 surveys. Though a general decrease of 22% occurred in the population, only a 12% decrease was found in the eight identical plots. Increases following conversion to hay production occurred in plots 5,16 (+46%) and 8,12 (+7%), even though an overall decrease occurred in the population. On the other hand, decreases much greater than 12% occurred in fields in which cattle were

Table 2. Changes in land use associated with percentage changes in population densities for plots surveyed in both 1976 and 1977.

Plot	Percentage Change in Population Density	Percentage Land Use[a] 1976	1977
5,16	+ 37.5	100h	100p
6,9	- 12.5	100h	100h
6,14	+160.0	85p,15h	65p,35h
7,4	+ 45.4	100h	100h
7,6	+ 85.7	100p	100h
9,9	+ 90.9	100h	20p,80h
9,25	+700.0	100p	85h,15p
10,10	+150.0	20w,80p	20w,80h
10,20	+ 50.0	100h	100h
11,17	+200.0	40w,60p	40w,60p

[a]h = hayfield, p = pasture, w = wooded.

Table 3. Changes in land use associated with percentage changes in population densities for plots surveyed in both 1977 and 1978.

Plot	Percentage Change in Population Density	Percentage Land Use[a] 1977	1978
5,12	0	65p,35h	65p,35h
5,16	+45.5	100p	15p,85h
6,9	0	100h	100h
6,14	-46.1	65p,35h	85p,15h
8,12	+ 7.1	50w,50p	50w,20p, 30h
8,21	-30.0	100h	100p
9,9	-42.9	80h,20p	80h,20p
11,8	-25.0	80h,20w	80h,20w

[a]h = hayfield, p = pasture, w = wooded.

introduced following the 1977 survey. A 30% decline occurred in plot 8,21 while a 46% decline occurred in plot 6,14.

In general, decreases in density occurred in fields switched from hay production to cattle grazing while increases occurred following a switch from pasture to hay. The above evidence supports the conclusion that competition between cattle and woodchucks and the distribution of habitat by the cattle caused woodchucks to leave a field when cattle were introduced and relocate in newly opened hay fields. On numerous occasions, cattle were observed pawing vigorously at entrance mounds, scratching their heads on entrances, and rolling in the dirt of the mounds. These actions tended to break down the entrances of the burrows and may have caused sufficient stress, prompting the woodchucks to leave the area and relocate elsewhere. In addition, it is felt that competition for forage occurred between the two animals. Thompson (1971) found that the species of vegetation browsed by cattle were similar to the preferred species utilized by woodchucks, and that in old field habitats in Kentucky all woodchuck dens were abandoned soon after cattle were introduced. However, in good pastures with high legume content, some woodchucks remained following cattle invasion.

The observation that woodchucks tend to leave areas when cattle move in is substantiated by woodchuck densities

for land use types during 1976 but not for 1977 and 1978 (Table 4). Perhaps, as densities rose, hayfields became saturated causing more woodchucks to remain in pastures in competition with cattle. Henderson and Gilbert (1978) found higher densities occurring in hayfields (8.4/ha) than in pastures (4.7/ha), though the highest densities were found in brushy fencerows (16.8/ha). Due to the patchiness of brushy areas in Cades Cove, densities were not calculated for this type of habitat; counts from brushy areas were included within the hayfields and pastures in which brush occurred. Thick cover along creekbeds was found to support many burrows, providing refuges for the population. High densities in these areas within pastures may have elevated densities enough to obscure lower populations in the open pastures.

During 1976 and 1978, densities were significantly higher in hayfields than in woodlots; but during 1977, when the population reached its highest level for the three years, there was no difference in the densities between the two areas. Henderson and Gilbert (1978), working in a high density area in Canada, also found no difference in hayfields (8.4/ha) and woodlots (8.8/ha). This indicates that at high densities, woodchucks move into wooded areas (particularly along the edge) and continue to utilize winter hibernation burrows during the summer.

Table 4. Comparison of mean densities of burrow systems in each land-use type for 1976, 1977, and 1978 (Mann-Whitney U-test, $p < .05$).

Year	Woodlots		Hayfields		Pasture
1976	0.64	<	1.55	>	0.84
1977	2.79	-	2.47	-	2.01
1978	1.24	<	2.11	-	2.01

< = significantly less than ($p < 0.05$).

> = significantly greater than ($p > 0.05$).

- = not significant.

Each year, the distribution of burrow systems for the entire Cove differed significantly from a Poisson distribution and the population was found to be aggregated. Clustering of burrows in many areas has been found to be related to soil texture (Moss 1940, Currier 1949, Anthony 1962). Silt loam soils comprise over 80% of the soils in Cades Cove making it unlikely that aggregations within the population were caused by soil texture. Well-drained soils and steep slopes have also been found to be prime factors in burrow location (Grizzell 1955, Merriam 1971); however, since the Cove floor is flat throughout with little change in topography and the majority of soils are well-drained, neither factor accounts for clustering of burrows. De Vos and Gillespie (1960) found that land

use practices influence burrow location. Vegetation differences, ground cover, and competition with cattle contribute to the high densities that occurred in hayfields and brushy areas in Cades Cove. Though densities were not calculated for brushy areas alone, burrows were often located in unmowed areas within hayfields and pasture and along creekbeds.

Another reason given for clumping in woodchuck populations is the mutual attractiveness that occurs among the woodchucks (Merriam 1971). Some areas in the Cove were lightly populated while other areas with similar soil composition, vegetation cover, and land use were more dense. Bronson (1963) concluded that low density groups had a much higher interaction rate as well as a greater frequency of down-alert behavior and a lower frequency of foraging behavior than high density groups. The low density groups appeared much more aware of their neighbors' actions and aggression levels were high (0.31 interactions per hour of activity), while a low aggression rate occurred in high density groups (0.10 per hour). Those animals in high density areas apparently take little notice of one another. Experiments conducted on visual contacts between woodchucks indicated that free-living animals determine the presence of others by primarily using visual cues (Bailey 1965b). Penned woodchucks given visual contact experienced weight gain closely resembling that of free-

living animals while those that were visually isolated exhibited a significantly lower gain. In addition, the greatest similarity in activity exhibited by woodchucks with visual contact occurred in the spring and early summer with seasonal changes in weight paralleled closely by changes in deposited fat (Snyder et al. 1961, Davis 1967a, 1967b, 1970), a factor crucial for hibernation.

Based on these facts, aggregations within a population appear to stimulate weight gain and reduce aggressive encounters. Woodchucks are better fit and forage more efficiently in close association with other woodchucks. Merriam (1971) attributed behaviorally-based spatial contagion to vestigial coloniality occurring in the woodchuck. Other closely related marmots have been found to exhibit varying degrees of coloniality with the woodchuck being the least social marmot (Barash 1974b).

When habitats were tested individually (woodlots, hayfields, pasture), clumping was found to occur only in the woodlots during 1977 and 1978. In 1976 only 13.5% of the sampled area fell in wooded areas with 44% of that area located within 20 m of the wood's edge. A total of 24.6% of the sampled area in 1977 was wooded with 30% lying in the transition zone while 24.7% of the quadrats sampled woods in 1978 with 26% being edge. In 1978, 67% of the burrows in the woods were in this transition zone compared to 63% in 1977 and 88% in 1976. The high

percentage of burrows found along the wood's edge in 1976 is a result of the greater proportion of area sampled there. Henderson and Gilbert (1978) found clumping in woodlots in Ontario to be related to the location of piles of cordwood and logs. This was found to be true in the Cove, but was limited primarily to the transition zone. In addition, the abundance of cover (Microstegium and Polygonum) in that area apparently was a key factor in attracting woodchucks. Within hayfields and pastures, woodchucks were distributed randomly.

Figure 3 illustrates the frequency distribution of the number of burrow systems per plot for each year. The population increased significantly from an estimated 814 to 1735 woodchucks between the summers of 1976 and 1977 (Mann-Whitney U-test, $p < 0.05$). The cattle herd in Cades Cove had been decreased by one-half during the summer of 1976 (Higgins, personal communication) and several fields which were changed from pasture to hay production for the first time in many years (Caughron, personal communication) were found to sustain the highest densities of woodchucks found in the Cove during the three years (4.0/ha). As competition with cattle appears to be a factor in the regulation of the woodchuck population in Cades Cove, the decline in the cattle numbers opened up new areas for increased woodchuck expansion.

A significant decrease from an estimated 1735 to

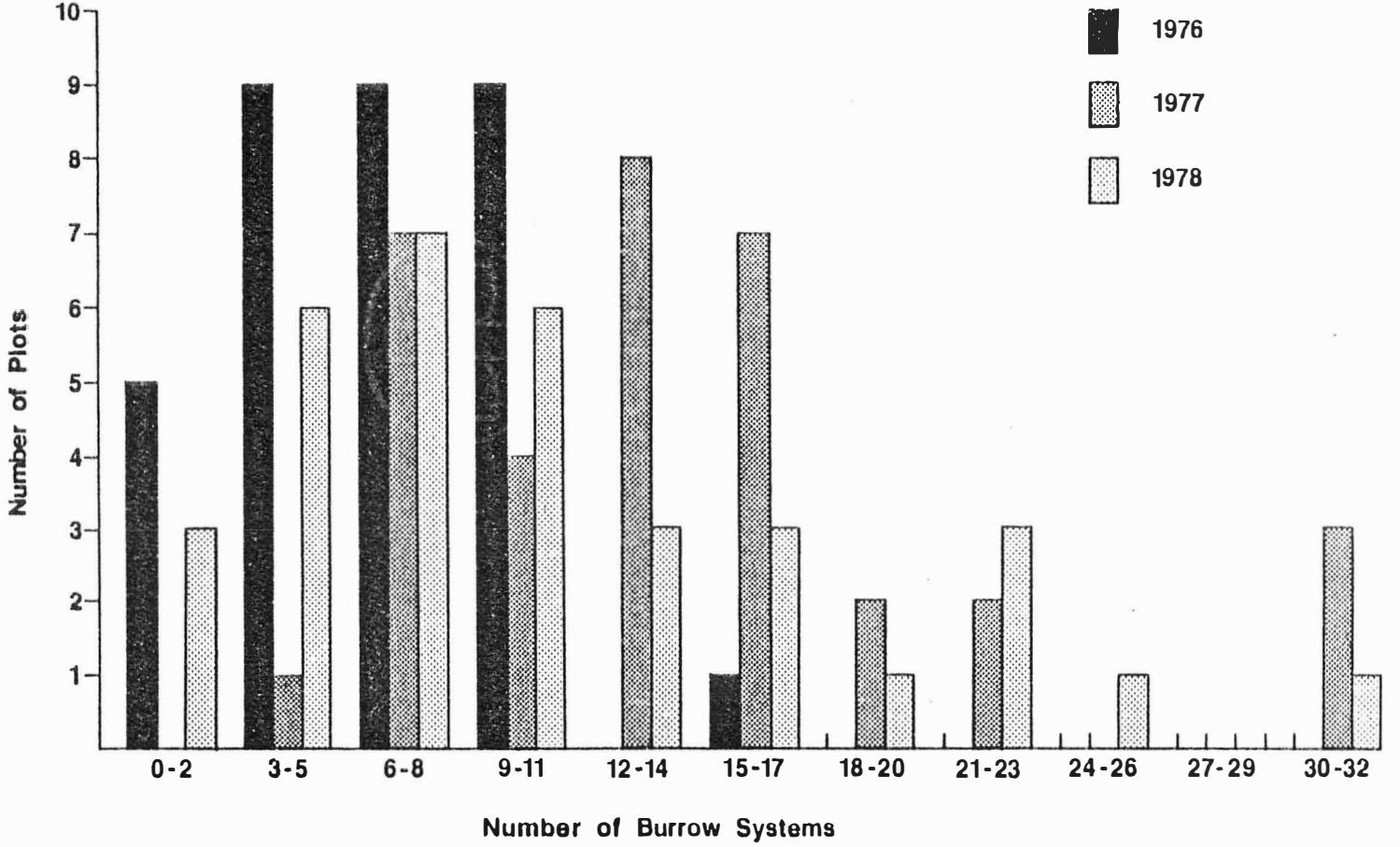

Figure 3. Frequency distribution of the number of burrows per plot in Cades Cove by year.

1351 woodchucks occurred in the population between 1977 and 1978 (Mann-Whitney U-test, $p < 0.05$). Fifteen carcasses were discovered during July and August, 1978 compared to two carcasses during the same period the previous year. Observations by researchers and reports by farmers, rangers, and park visitors, point to increased predation by wild dogs as a contributing factor. Predation by other animals, such as red and gray foxes, bobcats, bears, and hawks most certainly occurred, but no evidence points to increased predation by natural predators for that year.

Several researchers have remarked on breeding by yearling woodchucks (Hamilton 1934, Snyder 1962, Henderson and Gilbert 1978), though in unexploited populations, only 10-20% of the yearling females ordinarily breed (Grizzell 1955, Snyder 1961, 1962, Davis 1962, Davis et al. 1964). Therefore, the doubling in population size in Cades Cove between 1976 and 1977 resulted in a high proportion of yearlings in the population. If only a small percentage of those juveniles mated in 1978, natural mortality through the year might more than offset reproduction, causing a decline in the population. If this is the case, the population should surge upward in 1979, when the large cohort of two-year-olds begins reproducing. On the other hand, if competition with the cattle is the limiting factor, the population in 1977 may have increased to a

point above which it could efficiently compete, causing a decline to occur in 1978 to a more stable level. In that case, no significant change should occur in the population in 1979.

Burrow Dimensions

The average number of entrances per burrow, the average distance to the nearest active burrow, and the mound height decreased significantly from 1976 to 1977 while the mound diameter increased (Table 5). No difference was found in entrance diameter and distance to the nearest inactive burrow. Comparisons of burrow dimensions between 1977 and 1978 revealed significant increases in the average number of entrances per burrow, the number of regular entrances and the distance to an active burrow, while no changes occurred in the number of plunge entrances per burrow or in the distance to an inactive burrow. In addition, dimensions were taken for plunge and regular entrances during the 1977 survey and no differences were found between the two entrance types.

Of the variables taken during all three years, the number of entrances per burrow was shown to vary inversely with population size. Burrows that are utilized from year to year are normally modified with the addition of new entrances each year (Merriam 1971), while newly excavated burrows normally have only one or two entrances (Hamilton 1934, Merriam 1971, Henderson and Gilbert 1978).

Table 5. Comparison of means of burrow dimensions (t-test, $p < 0.05$) for woodchucks in Cades Cove, GSMNP.

Year	No. of Entrances	Dist. to Active Burrow (m)	Dist. to Inactive Burrow (m)	Entrance Diameter (cm)	Mound Height (cm)	Mound Diameter (cm)	No. of Plunge Entrances	No. of Regular Entrances
1976	3.32	40.53	39.72	17.60	11.09	65.00		
	*	*	ns	ns	*	*		
1977	2.85	31.19	40.63	18.01	5.70	73.78	1.28	1.54
	*	*	ns				ns	*
1978	3.26	40.33	56.25				1.15	2.16

* $p < 0.05$.

ns = not significant.

Therefore in an expanding population, such as that found in 1977, burrows would be newly dug, with few entrances. Then in 1978, when the population declined, few new burrows were required and new entrances and tunnels were added to existing systems. Most new entrances were regular entrances with mounds, as entrances of this type increased significantly while plunge entrances did not change.

An inverse relationship between population size and the mean distance between active burrows was also significant over three summers (t-test, $p < 0.05$). An increase in burrow systems caused more crowded conditions and therefore less distance between burrows. Bronson (1963, 1964) measured density as the mean distance between centers of activity, defined as the primary burrow system of an animal. As the distance between activity centers is negatively correlated with density, the mean distance between burrows increased when the population decreased in 1978.

Entrance dimensions showed no change from year to year, though mound diameters increased from 1976 to 1977 while mound heights decreased. No reason was evident for these changes.

The location of burrows in Cades Cove supports the idea that water is not a major concern. Many burrows were found at distances greater than 200 m from a water

source, which is a distance greater than that usually traversed by woodchucks (Twichell 1939, de Vos and Gillespie 1960, Merriam 1971, Henderson and Gilbert 1978). Many burrows, however, were located directly on creekbanks where the abundance of cover and shelter, along with the presence of soft soils, seemed to be major factors.

Other burrows were located on embankments along the road, indicating that the road system had little effect on numbers and distributions of woodchucks. Oxley et al. (1974) concluded that roads had little influence on movements of woodchucks but that mortality did increase with increasing road clearance. As the Loop Road in Cades Cove is a single-laned, one-way road, mortality due to cars should be minimal. A total of four road-killed woodchucks were observed by the author during the 14 months of study; thereby it was concluded that the road caused minimal interference.

A total of seven active burrows and three inactive burrows were found under barns and buildings in the Cove during the three surveys. One of the inactive burrows was found beneath a historical building that was frequented by park visitors, while the seven active burrows and the additional two inactive burrows were located beneath barns used for hay storage. Because so few burrows were found near buildings, particularly those visited regularly, it is concluded that historical

exhibitions and visitor usage in the Cove inhibited colonization by woodchucks.

Active systems for each year were grouped according to five habitat types. During 1976, the number of entrances per burrow for hayfields were found to be significantly greater than for those located in pastures (Table 6). No differences were found in entrance or mound diameters or in mound height among habitat types. The number of total entrances per burrow as well as the number of plunge entrances per burrow in 1977 was significantly less for burrows located in wooded areas than for all other habitats while no difference was found in the number of main entrances. These burrows had few entrances ($\bar{X}$ = 1.9) which by necessity, were main entrances. Entrance diameters were found to be greater in hayfields and brushy areas than in pastures and woods while mound heights were greater in woods than those in brush, hayfields, and pasture. Mound diameters were similar in all habitats. The burrows located in pasture had the most entrances per burrow in 1978, and burrows in hayfields had more than those in woods. Burrows in pastures also had a greater number of both main and plunge entrances than any other habitat type. No other differences were found in the number of main entrances while more plunge entrances were found per burrow in hayfields than in brush and woods.

Table 6. Comparison of burrow dimensions by habitat[a] for 1976, 1977, and 1978.

Burrow Dimensions	Means of Burrow Dimensions				
	1976				
No. of entrances	3.73 (H)	3.00 (W)	2.88 (Br)	2.86 (P) [b]	
Entrance diameter (cm)	18.44 (Br)	17.98 (H)	17.83 (W)	16.86 (P)	
Mound height (cm)	14.18 (W)	12.14 (Br)	11.97 (P)	10.02 (H)	
Mound diameter (cm)	66.68 (H)	64.86 (W)	63.53 (P)	56.60 (Br)	
	1977				
No. of entrances	5.00 (Bg)	3.42 (H)	2.99 (P)	2.77 (Br)	1.95 (W)
No. of main entrances	2.00 (Bg)	1.65 (H)	1.52 (Br)	1.49 (W)	1.40 (P)
No. of plunge entrances	3.00 (Bg)	1.78 (H)	1.56 (P)	1.12 (Br)	0.47 (W)
Entrance diameter (cm)	18.48 (H)	18.18 (Br)	17.90 (Bg)	17.41 (W)	17.05 (P)
Mound height (cm)	7.01 (W)	7.00 (Bg)	5.52 (Br)	5.38 (H)	4.46 (P)
Mound diameter (cm)	78.27 (W)	72.80 (P)	72.14 (Br)	71.92 (H)	65.00 (Bg)
	1978				
No. of entrances	4.08 (P)	3.19 (H)	3.00 (Bg)	2.73 (Br)	2.26 (W)
No. of main entrances	2.50 (P)	2.04 (H)	2.00 (Bg)	1.92 (Br)	1.74 (W)
No. of plunge entrances	1.79 (P)	1.03 (H)	1.00 (Bg)	0.45 (Br)	0.41 (W)

[a]Duncan Multiple Range Test, $p < .05$. H = hayfields, P = pasture, W = woodlots, Br = brush, Bg = building.

[b]Underscoring denotes no significant differences between connected numbers.

No trends developed in burrow dimensions among the various habitats. The number of total entrances per burrow was greater for hayfields than for pasture during 1976. The following year, burrows in wooded areas had fewer entrances than in either hayfields or pasture and during the third year, more entrances per burrow were found in pasture than in hayfields which had more than those in woods. The same apparent random changes occurred in other dimensions.

The average number of entrances found per year (3.32, 2.85, 3.26) is slightly higher than the 2.8 entrances reported by Twichell (1939) and the 2.98 entrances found by Merriam (1971) while entrance diameters of 17.6 cm and 18.0 cm fall within the 10.5 to 34.0 cm widths reported by Grizzell (1955). Grizzell found that plunge holes were typically smaller than main entrances, a finding not supported by the present study.

Soil Analysis

Burrow locations have been found to be closely associated with soil textures such as sandy loams (Moss 1940), fine sandy loams (Currier 1949), and silt loams (Anthony 1962). In the present study, burrows were located predominantly in areas with silt loam soils (Table 7). This soil type makes up approximately 80% of the soils found in Cades Cove (Elder et al. 1959).

Table 7. Frequency distribution for burrows located in soils of varying textures.

	Percent					
Year	Silt Loam	Silty Clay Loam	Loam	Silty Loam	Fine Sandy Loam	Stony Colluvial
1976	79.0	4.1	12.8	0.0	2.7	1.4
1977	81.9	3.9	7.2	2.3	2.4	2.3
1978	87.8	5.7	3.0	0.0	2.0	1.5

Well-drained soils are also a prime factor determining burrow location (Grizzell 1955, Merriam 1971). The location of burrows in Cades Cove supports that hypothesis (Table 8), though again, well-drained soils are predominant in the Cove.

Table 8. Frequency distribution of soil drainage classes for burrow systems in Cades Cove.

	Percent			
Year	Well-Drained	Moderately Drained	Imperfectly Drained	Poorly Drained
1976	77.4	10.1	10.6	1.9
1977	82.5	8.7	5.2	3.6
1978	75.3	13.3	7.2	4.2

II. BEHAVIORAL ANALYSIS

Seasonal and Daily Effects on Activity

Effects of time of year were noted in both total activity and in frequencies of different behaviors. The mean number of woodchucks observed per hour by month illustrates the changing activity levels throughout the year (Figure 4), reflecting the population density of non-hibernating woodchucks, as well as the activity levels of individuals. No woodchucks were observed during the month of January; however, signs of activity such as tracks, fecal matter, and cleared entrances were found. Linzey and Linzey (1971) reported sightings throughout the year in the Park, though the animals were rarely seen in extremely cold weather. These signs and sightings of woodchucks on sunny days in January indicate that the animals may arouse occasionally during hibernation in order to defecate. It is well known that hibernating animals awaken periodically when the byproducts of metabolism build up in their bodies to near toxic levels. A few deep breaths of fresh air and an increase in kidney function allow the blood chemistry to return to normal homeostatic levels (Mrosovsky 1971, Kelsey 1978).

The mean number of woodchucks observed per hour increased rapidly in February and March as adults, then juveniles, emerged from hibernation. The proportion of foraging that occurred in February was much lower than

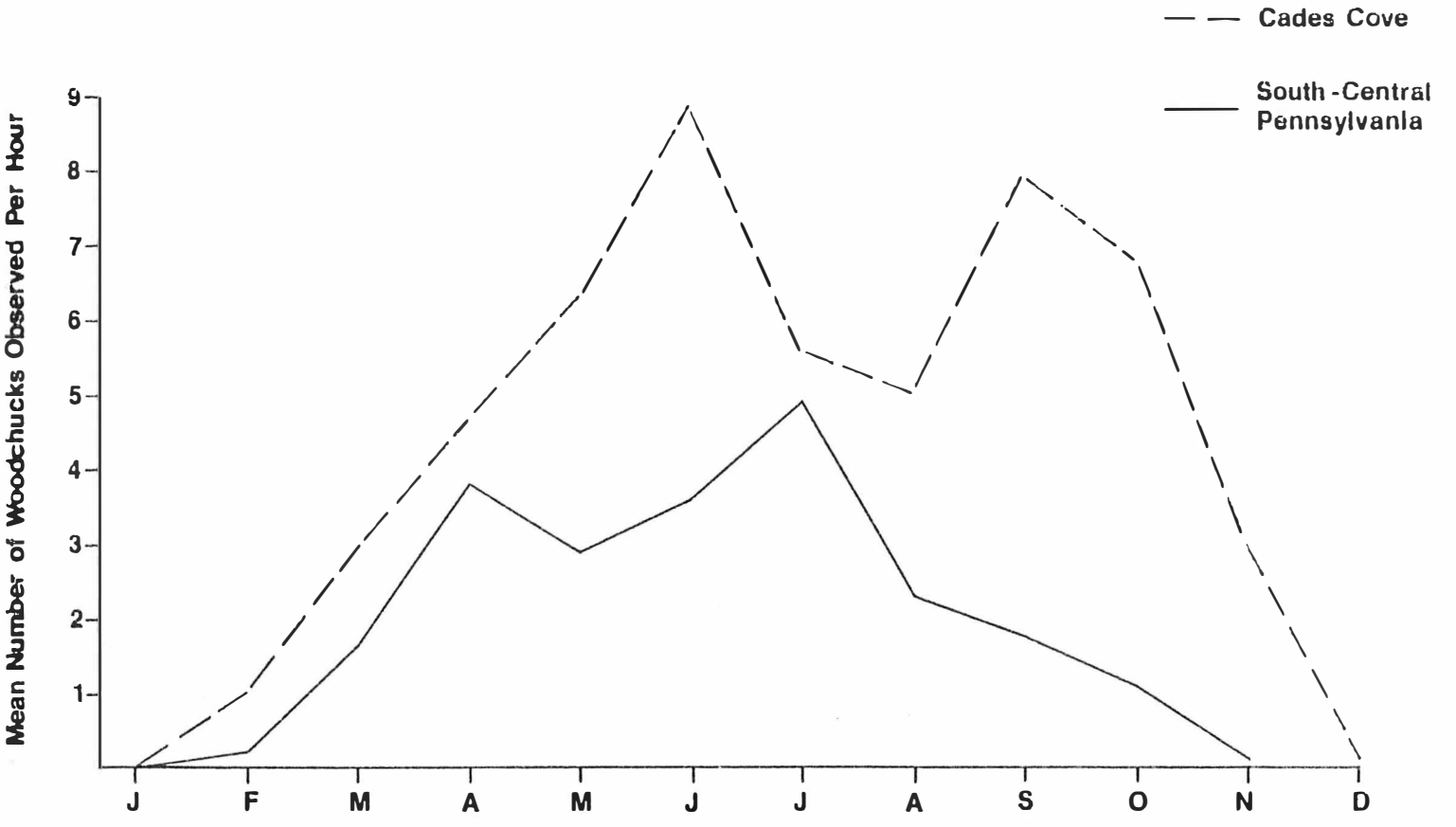

Figure 4. Comparison between the mean number of woodchucks observed per hour by month in Cades Cove, GSMNP (present study), and southcentral Pennsylvania (from Bronson 1964).

that which occurred in the subsequent months (Table 9), due to the fact that little feeding takes place in the first two to three weeks following hibernation (Snyder and Christian 1960). Additional increases in activity in March and April were a result of increased activity per individual as foraging became the major activity. Young of the year were first observed emerging from their natal burrows in late April and appeared in increasing numbers in May. Dispersal of the young occurred in late May and June, causing a surge in population density and the highest levels of activity for the year (Figure 4). Activity levels declined in July and August as juveniles may have dispersed outside of the observed areas thereby lowering the population. Snyder (1961, 1962) and Armitage (1965) have documented that juveniles are often forced to disperse out of the area in which they were born, a mechanism that prevents overpopulation. Other young had undoubtedly located home burrows and were less visible. Foraging constituted a relatively low proportion of activity during these months, indicating lowered foraging pressures due to the readily available food supply (Table 9).

A second peak in mean activity occurred in September and October and was likely a result of increased individual activity. The proportion of foraging increased in September contributing to increased fat accumulation, a phenomenon

Table 9. Frequency distribution of behaviors exhibited by woodchucks in Cades Cove, GSMNP, by month.[a]

Month[b]	No. of Observations Per Month	Percent					
		Up-Alert	Down-Alert	Foraging	Resting	Traveling	Misc.
Jan.nt	60	0	0	0	0	0	0
Feb.*	117	1.12	40.90	46.29	2.70	5.84	3.15
March*	211	1.69	28.69	64.91	0.38	2.57	1.76
April*	526	4.28	34.74	55.75	0.79	3.01	1.43
May*	630	8.71	31.66	51.27	0.84	2.73	4.70
June*	500	14.85	29.43	52.33	0.31	1.84	1.23
July*	789	34.02	22.23	40.07	0.81	0.95	1.92
Aug.*	706	36.30	9.38	50.75	1.34	0.94	1.29
Sept.*	622	23.22	20.40	54.18	0.14	1.47	0.59
Oct.*	430	26.79	27.91	42.58	0.33	1.38	1.01
Nov.nt	384	17.56	30.64	48.20	0.37	1.45	1.78
Dec.nt	132	0	41.86	55.81	0	2.33	0

[a]The distribution for each month was tested for homogeneity with the succeeding month (Chi Square Test for Goodness of Fit, $p < 0.05$). The behavior of each woodchuck observed during a scan survey was recorded as that behavior observed when first observed.

[b]nt = sample size of animals observed was too small to be tested; * = $p < 0.05$.

documented by Bailey (1965a) and Davis (1967a). Food consumption and weight gain by woodchucks have been shown to increase in late autumn (Bailey and Davis 1965, Fall 1971). Davis (1971) and Davis and Finnie (1975) demonstrated an endogenous circannual rhythm of food intake which accounts for these increases.

Activity declined rapidly after October as population density decreased due to mortality, the food supply became limited, and woodchucks entered hibernation. A decrease in foraging has been found to occur two to three weeks prior to hibernation (Barash 1976), which explains the decline in the frequency of foraging in October and November (Table 9). By mid-December, activity was sporadic and minimal (Figure 4).

An activity pattern reported by Bronson (1962) for south-central Pennsylvania follows a similar schedule though offset by one month due to later emergence from hibernation (Figure 4). He attributed a decrease that occurred in May to vegetational interference on visibility, a factor that was minimal in the present study. Similar peaks occurred during juvenile dispersal, though again a month separates the two studies. The lack of a second peak in the Pennsylvania cycle is likely due to the shorter growing season and to the onset of hibernation at an earlier time (approximately one month).

The mean number of woodchucks observed per hour by

season illustrates that the greatest increase occurred in the spring when the adults emerged from hibernation and the young first appeared. This increase continued through the summer as young emerged in greater numbers and dispersed into the population. Activity reached a peak in the fall as foraging increased, then dropped rapidly to the low levels found in winter (Figure 5). The seasonal divisions were determined independently of woodchuck activity and were set according to vegetational development, breeding behavior, and dispersal of young. Divisions occurred in mid-February, mid-May, mid-September, and mid-November, delineating the beginnings of spring, summer, fall, and winter, respectively. These divisions were used in all seasonal analyses.

The distribution of behaviors for each season was found to differ significantly from all other seasons (Table 10). Foraging was the dominant behavior during the spring, occurring 56.5% of the time; it then dropped to a relatively constant 48% for the summer, fall, and winter. A state of alertness was found to represent interruptions of ongoing foraging behavior, and therefore would be expected to change inversely in proportion to foraging. This condition was found to exist as the frequency of alertness was lowest in the spring (37.7%) when the frequency of foraging was highest. During the summer, fall, and winter, alertness varied more than

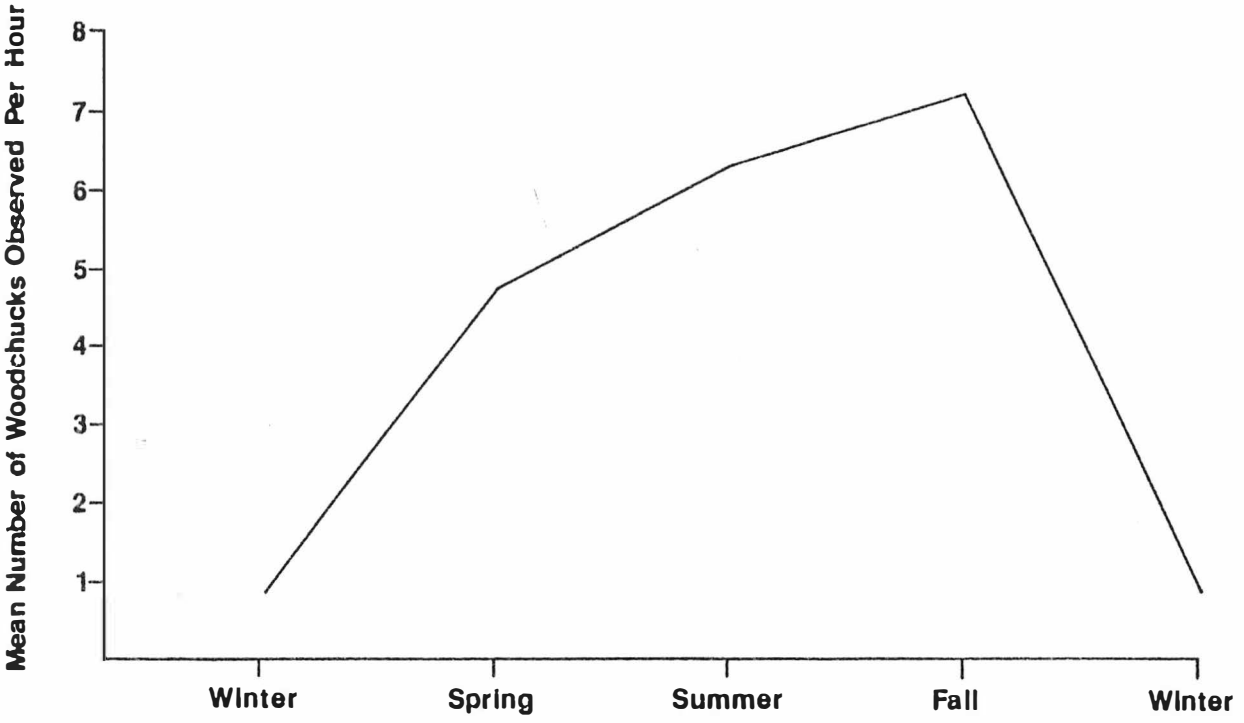

Figure 5. Mean number of woodchucks observed per hour by season in Cades Cove, GSMNP.

Table 10. Total numbers of woodchucks observed in each behavior category and the average proportion of time devoted to each by season.[a]

	Season	Up-Alert	Down-Alert	Foraging	Resting	Traveling	Misc.	Total
Total Woodchucks	Spring	383	2607	4529	63	228	151	7961
	Summer	4413	3906	8500	125	256	373	17573
	Fall	2685	2698	5255	27	151	92	10908
	Winter	15	267	328	12	29	25	676
				Percent				
Proportions	Spring	4.81	32.75	56.89	0.79	2.86	1.90	
	Summer	25.11	22.23	48.37	0.71	1.46	2.12	
	Fall	24.62	24.73	48.18	0.25	1.38	0.84	
	Winter	2.22	39.50	48.52	1.78	4.29	3.70	

[a]The distribution of behaviors for each season differs from every other season; $p < 0.05$.

foraging due to increases in the minor categories: resting, traveling, and miscellaneous.

Dividing alertness into its two components of up-alert and down-alert reveals that up-alert was very low for winter and spring and was nearly equal to down-alert during the summer and fall. The frequency of up-alert increased as the days grew longer and the hay in the fields grew taller. Several woodchucks resorted to climbing fenceposts and tree stumps for use as look-out posts, an activity that contributed to the miscellaneous category in the summer and fall. Following haying operations in early June and mid-August, the frequency of up-alert declined. Alertness, in general, was greatest in the summer and fall as the woodchucks had to exert more energy to maintain a watchful eye on their surroundings. The interference of vegetation on observations was kept to a minimum by disregarding those where interference was a major factor. The practice of cutting the hay twice during the summer by the leasee aided in minimizing interference.

Another notable change in frequency occurred in the amount of movement between burrow systems. Though fairly constant for most of the year, traveling more than doubled during the spring. No mating was observed, but it is likely that these movements were a result of males searching for suitable mates. Schoonmaker (1966)

stated that in the spring the males may cover a large area in search of mates, while the females remain near their dens.

Resting behavior was constant for spring and summer (0.70 and 0.71) but decreased during the fall, possibly due to increased foraging pressures. During the winter, however, time spent resting was much higher as woodchucks may have aroused from hibernation and sunned themselves on their mounds on warm winter days.

Miscellaneous behaviors were exhibited more often during the winter than during any other season. A breakdown into the component behaviors illustrates that burrow maintenance comprised most of this category (Table 11).

Table 11. Seasonal frequency distributions of the five components of the miscellaneous behavior category.

		Percent				
Season	N	Burrow Maintenance	Grooming	Social Interactions	Agonistic	Fence Climbing
Spring	165	0.09	0.48	1.03	0.21	0.04
Summer	373	0.02	0.10	0.05	0.06	0.17
Fall	92	0.25	0.11	0.09	0.14	0.12
Winter	11	2.00	0.44	0.59	0.59	0

N = the number of animals observed exhibiting the five miscellaneous behaviors.

Bundles of dried grass were collected and carried into the burrow and were probably used as nesting material. Twichell (1939) documented the use of leaves and grass in hibernation nests. Burrow maintenance may also include the removal of dirt and debris from the burrow, and though it was seldom observed, signs of this activity were common throughout the year.

The most frequent miscellaneous behavior in the spring was social interaction. Early in the spring, males and females mate and may cohabit a single burrow until prior to birth of the young when the male is driven out (Bronson 1964, Schoonmaker 1966). Once the young in Cades Cove were a few weeks old and left the confines of the burrow, they were observed frequently in close association with the female and their siblings. As dispersal did not occur until late May and June, these familial ties elevated the observance of social interactions during the summer. Agonistic behavior was frequently observed between the female and her young at the time of dispersal (Table 11) and supports evidence that weaning and dispersal are accompanied by elevated aggression between the female and her young (Barash 1974a, 1974b). Shortly after this period, two woodchucks were occasionally observed utilizing the same burrow and due to their small size, it was assumed that they were siblings. Grooming behavior occurred most frequently in

the spring as scratching and biting aid in removal of the heavy winter pelage.

The frequency distribution of behaviors exhibited by woodchucks observed in the Cades Cove population was significantly different from those exhibited by populations in New York (Conrad and Fidura 1970) and Pennsylvania (Bronson 1962) during comparable time periods (Chi Square Goodness of Fit, $p < 0.05$). In both northern populations, foraging constituted a much higher proportion of activity (Spring: New York 78%, Tennessee 57%; summer: Pennsylvania 72%, Tennessee 48%). The abundant food supply and longer growing season in Cades Cove contributed to the decreased foraging pressures in this southeastern extremity of the woodchucks' range. Social interaction and agonistic behavior were very low in all three studies, supporting theories that the woodchuck is an asocial animal.

It was observed that, in addition to changes in relative activity and behavioral frequencies, daily activity patterns changed through the year. Early (February through mid-April) and late (September through December) in the year, activity occurred predominantly midday, resulting in a unimodal distribution for the months of February through March and September through November (Figure 6). A trend of bimodal distribution began to develop in April with peaks occurring in activity

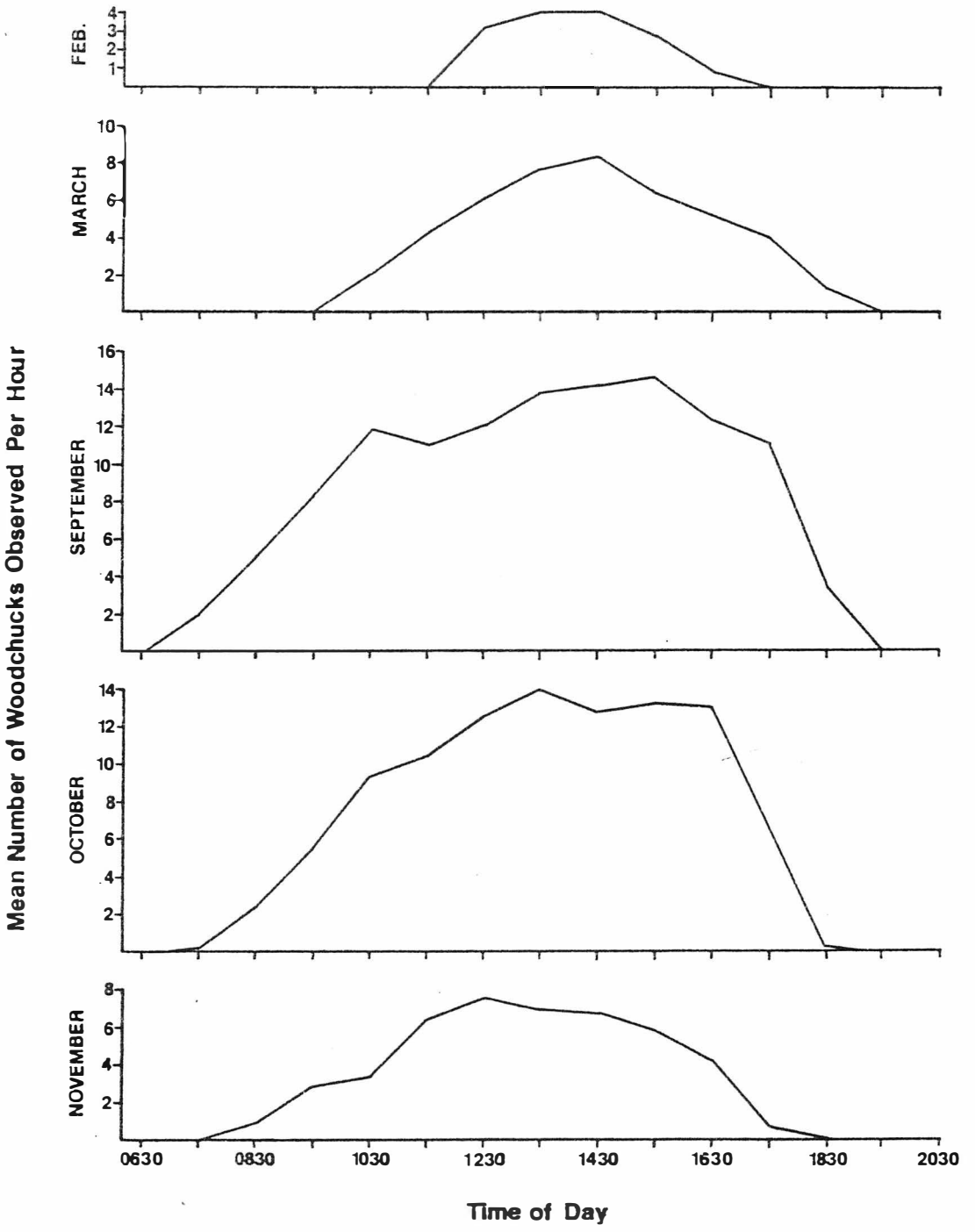

Figure 6. Daily activity patterns of woodchucks in Cades Cove, GSMNP, for months having a unimodal distribution.

around 1100 hours and 1600 hours (Figure 7). This gap widened with an increase in day length until June and July, when peaks occurred at 0900 and 1800 hrs. The opposite trend began to occur in August with a convergence into a unimodal distribution in September; this pattern continued until activity ceased in late December. The distribution for each month, when tested against the succeeding month, was significantly different for all combinations except June and July, with significant Chi Square values ranging from 47.2 to 137.3. November, December, and January were not tested against the following months due to low activity levels. The similarity in the June and July distributions is probably due to the similarity in environmental variables at that time, particularly in day length.

The distributional differences that occurred in activity patterns by month became more pronounced when activity was grouped into seasons (Figure 8). Fall and spring distributions of activity were basically unimodal, though a slight indication of bimodality occurred in the spring, due to the inclusion of late April and early May. A bimodal distribution was very strong during the summer, a pattern attributed by several researchers to high temperatures (Armitage 1962, Conrad and Fidura 1970, Hayes 1976). However, in this study, activity was shown to be not significantly affected by temperature during the

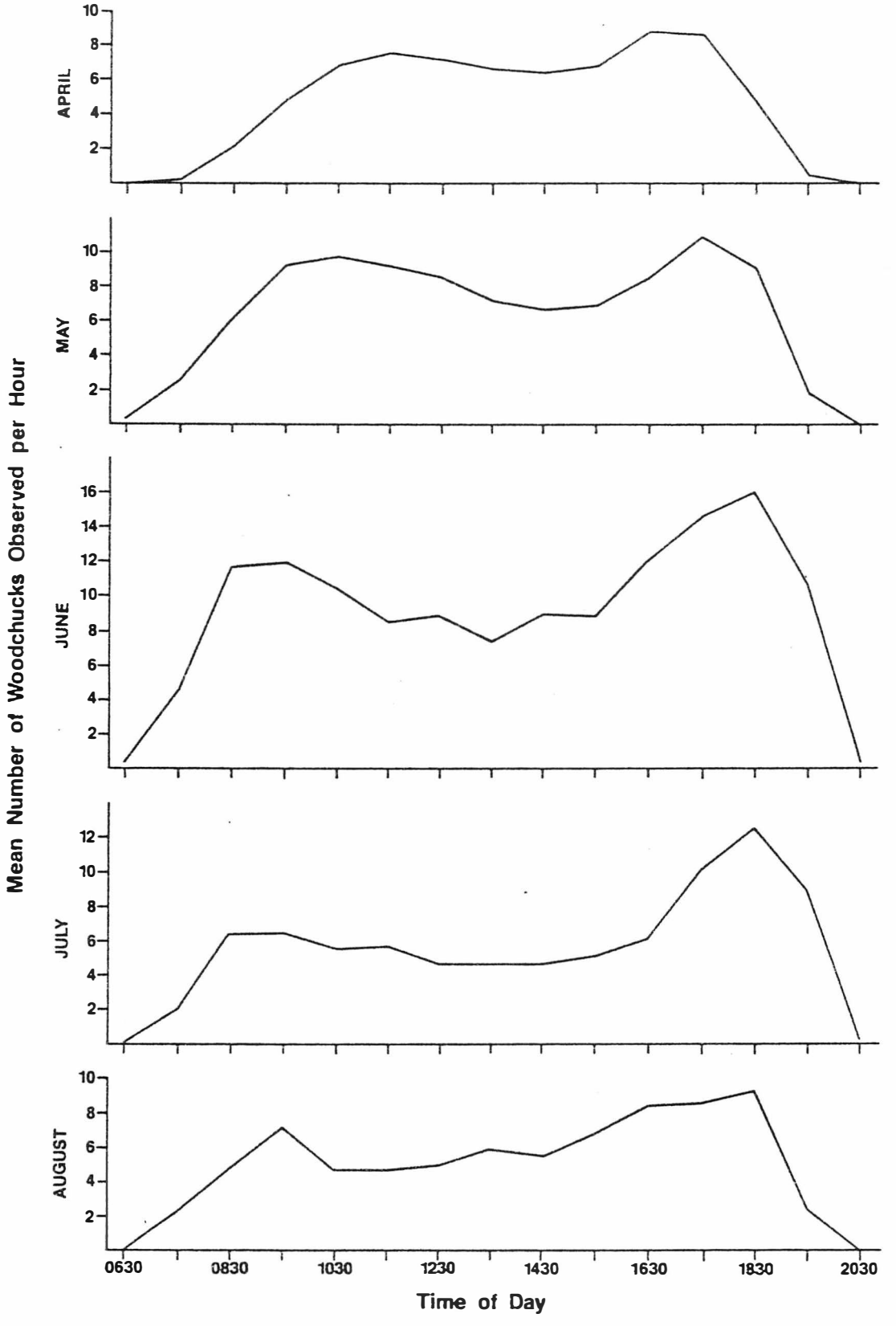

Figure 7. Daily activity patterns of woodchucks in Cades Cove, GSMNP, for months having a bimodal distribution.

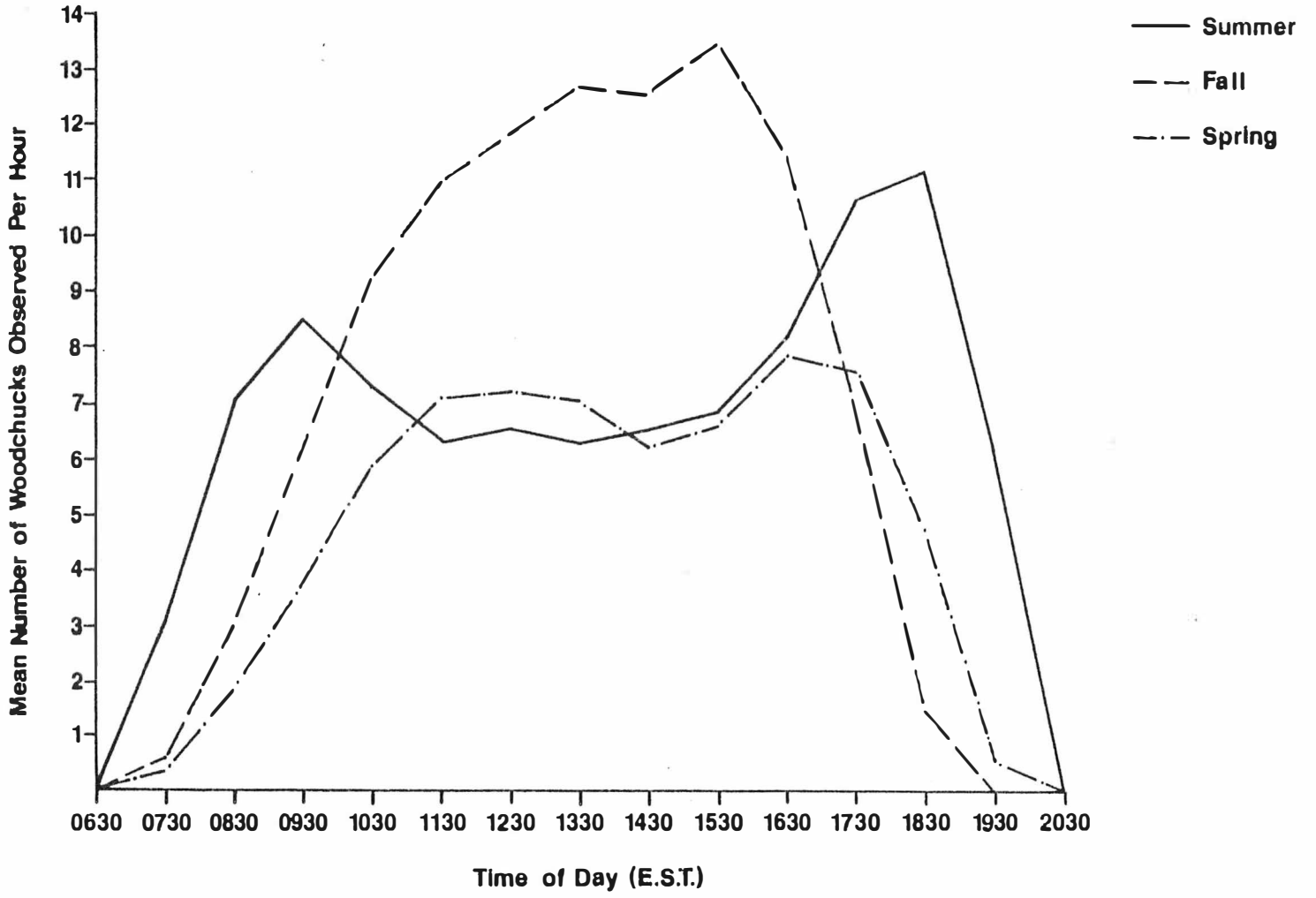

Figure 8. Seasonal activity patterns of woodchucks in Cades Cove, GSMNP.

summer (p. 64). Further evidence is given in Table 12 which lists the range of maximum temperatures for days of observation by month. The mean maximum temperature for May, a month in which activity was distinctly bimodal, was 4.7° C lower than the mean maximum temperature for September, a month in which activity exhibited a unimodal distribution. Therefore, inhibition of activity at temperatures above 31° C, as suggested by Hayes (1976), is thought not to be the case with this population.

The decline in midday activity during the summer did not appear to be as drastic in the Tennessee population as that reported in more northern populations (Bronson 1962, Conrad and Fidura 1970). The abundant vegetation available in the Cove, and relaxed foraging pressures allowed activity to spread more evenly throughout the day. A relationship between time of day and activity levels during the summer was shown and was probably involved in creating bimodality. Armitage (1962) suggested defecation as the stimulus for emergence, followed by 15-30 minutes of sunning and grooming. Since all woodchucks would have been affected by this "urge," activity levels would be relatively higher in the early morning. Bronson (1964) found individual woodchucks to be active for approximately three hours a day resulting in a small proportion of the population being active at any one time during the day. Coupled with relaxed foraging

Table 12. Mean maximum temperatures, ranges of maximum temperatures, and daily distribution patterns for observations day by month.

Month	Number of Observation Days	Range of Maximum Temperatures	Mean Temperature	Distribution Pattern
January	3	-7 to 16°C	1.7°C	-
February	5	-2 to 8	4.7	Unimodal
March	6	1 to 21	9.3	Unimodal
April	9	16 to 28	23.2	Bimodal
May	7	11 to 28	20.9	Bimodal
June	6	27 to 33	30.3	Bimodal
July	10	28 to 37	31.6	Bimodal
August	9	26 to 32	29.8	Bimodal
September	9	21 to 30	25.6	Unimodal
October	7	13 to 23	19.1	Unimodal
November	8	7 to 26	18.6	Unimodal
December	5	-1 to 12	8.1	Unimodal

pressures and long summer days, this fact would cause lowered activity during midday as supported by this study. However, as summer days are slightly shorter in Cades Cove than in the more northern areas, more woodchucks would be active at any one time, resulting in a less drastic midday slump in activity. The observed increase in activity shortly before sunset may have been prompted by lower light intensity stimulating the woodchucks to feed and store up energy for the night.

Activity levels and behavioral frequencies varied in a regular pattern on a daily basis. Significant differences were found in the distribution of behavioral frequencies for the morning (0600 hrs to 1300 hrs) and the afternoon (1300 hrs to 2100 hrs). Alert activities, including both the up-alert and down-alert positions, were predominant during the first half of the day while foraging comprised the majority of activity during the latter period (Table 13). This pattern was evident for all seasons and was also found to occur in New York (Conrad and Fidura 1970) and Pennsylvania (Bronson 1964). Resting behaviors occurred about twice as frequently before midday as after, and miscellaneous activities also occurred more often in the morning. No differences were found to occur in the rates of traveling for the two time periods.

Armitage (1962) postulated that defecation is the

Table 13. The number of woodchucks observed in each of six behavior categories, and the relative proportions of time devoted to each behavior, by time of day.[a]

Time of Day	Statistics	Up-Alert	Down-Alert	Foraging	Resting	Traveling	Misc.	Total
0600-1300 hours	total wc[b]	3273	4593	6540	135	257	329	15127
	frequency	21.64%	30.36%	43.23%	0.89%	1.70%	2.18%	
1300-2100 hours	total wc	4273	4888	12072	92	407	312	21994
	frequency	19.20%	22.22%	54.89%	0.42%	1.85%	1.42%	
Total	total wc	7496	9481	18612	227	664	641	37121
	frequency	20.19%	25.54%	50.14%	0.61%	1.79%	1.73%	

[a]A Chi Square analysis showed a significant difference between morning and afternoon activity levels ($p < 0.05$).

[b]wc = woodchucks.

stimulus for emergence, with sunning and grooming behavior commonly following that activity. Though defecation was not discernible in the present study, resting (synonymous with sunning), alert, and miscellaneous behaviors (including grooming, burrow maintenance, and social interactions) were common following emergence. The woodchucks may have tested their environmental and social surroundings at this time while foraging apparently began only after the local situation was evaluated.

Climatic Effects on Activity

Four climatic variables were recorded in this study (ambient temperature, relative humidity, percentage cloud cover, and precipitation) and all but relative humidity were shown to significantly affect activity over a period of one year (Table 14). However, when tested within a season, these same variables were not always significant (Table 15). Considerable relationships existed both among the variables themselves and between the variables and various biological conditions (food supply, circannual and circadian rhythms, and reproductive condition). These interrelationships among variables complicated the testing of hypotheses concerning cause and effect relationships between climatic factors and activity behavior. This situation was particularly true with relative humidity.

When the partial sums of squares of relative

Table 14. Analysis of variance for activity of woodchucks in Cades Cove, GSMNP, with respect to time of year, time of day, and climatic factors for a year period.

Source of Variance	df	SS	Sequential SS	F	df	Partial SS	F
Total	102	28020					
Date	68		17734	14.23*	68	13758	11.04*
Interval	27		7603	15.36*	27	2340	4.73*
Cloud Cover	1		647	35.32*	1	1157	63.13*
Temperature	1		922	50.29*	1	248	13.53*
Relative Humidity	1		96	5.26*	1	7	0.37ns
Precipitation	4		1018	13.88*	4	1018	13.88*

*$p < 0.05$.

ns = not significant.

Table 15. Analysis of variance for activity behavior of woodchucks in Cades Cove, GSMNP, with respect to time of year, time of day, and climatic factors for winter, spring, summer and fall.

Source of Variance	Winter					Spring					Summer					Fall				
		Type I		Type III			Type I		Type III			Type I		Type III			Type I		Type III	
	df	SS	F	SS	F	df	SS	F	SS	F	df	SS	F	SS	F	df	SS	F	SS	F
Date	9	503	34.37+	288	19.69+	18	4865	18.62+	1969	7.54+	22	4720	15.17+	3876	12.46+	16	2861	10.00+	2625	9.18+
Interval	15	15	.62-	19	.76+	26	2143	5.68+	1034	2.74+	27	4486	11.75+	3588	9.40+	24	7189	16.76+	2278	5.31+
Cloud Cover	1	1	.65-	.02	.02-	1	14	.97-	59	4.09+	1	423	29.90+	593	41.94+	1	53	2.99-	152	8.53+
Temperature	1	15	9.04+	.31	.19-	1	104	7.18+	20	1.40-	1	85	5.98+	4	.30-	1	34	1.89-	16	.91-
Rel. Hum.	1	9	5.60+	12	7.16+	1	42	2.93-	5	.33-	1	123	8.69+	65	4.62+	1	6	.32-	22	1.22-
Precip.	3	5	.94-	5	.94-	4	231	3.98+	230	3.98+	3	261	6.15+	260	6.15+	3	1015	18.93+	1015	18.93+

+ = $p < 0.05$.

- = non-significant.

humidity were tested for the year, the F value was not significant. However, a strong relationship with precipitation was suggested by the significance of the sequential sums of squares when relative humidity preceded precipitation (Table 14). This means that relative humidity could explain a significant portion of the variation in activity only if the precipitation level was unknown. Once the latter variable was considered, no additional variation in activity could be explained by relative humidity. However, when tested within each season, activity was found to be inversely proportional to relative humidity in the summer and winter, but no relationship was apparent in the spring and fall (Table 15). This fact suggests that relative humidity only affected woodchucks at the extremes of the temperature range. When temperatures were above the thermal neutral zone of the organism and a high relative humidity existed, heat loss through sweat evaporation was minimal so the animals would probably have been less active. The opposite might have occurred in winter when the ambient temperature was far below the body temperature of the organisms and moisture increased heat loss. Hibernation and underground activity would apparently minimize heat loss.

The effects of precipitation on activity are clear. For all seasons except winter, increasing precipitation caused diminished activity. A slight rain resulted in a

slight decrease while a moderate or hard rain normally caused a cessation of above-ground activity. Snow and sleet also inhibited activity. No effect was apparent during the winter due to low levels of activity.

Increasing cloud cover resulted in increased activity during the spring, summer, and fall. This effect could be due to decreased effects of solar radiation at the surface of the animal. The effect of cloud cover appears to be greatest during the summer when solar radiation would also be the greatest. Again, no effect was found in the winter when activity was very low and sporadic, and time of year appeared to be the major factor.

The effect of ambient temperature was found not to be significant within any season even though it was significant among seasons (Tables 14 and 15). The variation in temperature within any season is small compared to the whole year. Therefore activity can be significantly affected by the changes in temperature on a yearly basis without being affected within a particular season. Inhibition of activity at temperatures above 31° C, as suggested by Hayes (1976), was not found in this study.

CHAPTER IV

CONCLUSIONS

The major conclusions of this study were directed in response to the four primary objectives. They included the following:

1. Diurnal observations resulted in the conclusion that 75% of all active woodchuck burrow systems in Cades Cove were utilized by permanent residents. Therefore, the population was estimated to be 814, 1735, and 1351 woodchucks for 1976, 1977, and 1978, respectfully.

2. The population was found to be aggregated for all three years and within woodlots during 1977 and 1978. Clumping occurred in response to land-use patterns, the edge effect of the woods, and social interaction. No clumping was evident within pasture and hayfield. Competition with cattle, predation, and social interactions were major factors influencing population numbers. Water, roads and soils did not affect burrow location while buildings and historical exhibitions inhibited colonization. The mean number of entrances per burrow and the mean distance between active burrows varied inversely with population size. No significant differences existed in burrow dimensions between years or between habitat types.

3. Activity levels of woodchucks varied through the year due to the changing density of non-hibernating animals and to the changing activity levels of individuals. Mean levels of activity observed per hour increased from February through June as woodchucks emerged from hibernation, individual activity increased, and young appeared, then dispersed. Relaxed foraging pressures and location of home burrows by juveniles resulted in a decline in activity through August, followed by increased foraging pressures and increased activity levels in September and October. Activity rapidly declined in November and December as woodchucks entered hibernation. This pattern resembled activity in Pennsylvania, shifted slightly due to shorter duration of hibernation in the Southeast.

Daily activity patterns changed through the year, a unimodal distribution occurring from February through mid-April and September through December while a bimodal distribution occurred from mid-April through early September. The bimodal response did not occur due to inhibition of activity at temperatures above 31° C as suggested by an earlier study. Precipitation, cloud cover, and temperature affected activity over a one-year period, while relative humidity did not. However, the effects of climatic factors varied according to season. The effects of precipitation were negative for the spring, summer, and fall, while no effects were evident in the

winter. Increased cloud cover resulted in increased activity in the spring, summer, and fall, and again no effects were apparent during the winter. Temperature did not affect activity within any season, though relative humidity inhibited activity during the summer and winter but had no effect during the spring and fall.

4. The frequency distribution of the various behaviors shifted seasonally. Foraging constituted the dominant behavior in all seasons, and varied inversely with alertness as the latter represented interruptions in foraging. Behavioral changes occurred primarily in response to reproductive condition, environmental conditions, and social interactions. The frequencies of different behaviors also changed according to time of day. Resting, alertness, traveling, and miscellaneous behaviors were more prevalent during the morning hours, while foraging was predominant during the afternoon.

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VITA

Cathy A. Taylor was born on 5 May 1954, in Davenport, Iowa. She attended elementary schools in Bettendorf, Iowa, Mount Lebanon, Pennsylvania, and Maryville, Tennessee. It was in the latter city that she received her high school diploma from Maryville High School in June 1972. Upon entrance to The University of Tennessee, Knoxville in September 1972, she enrolled in the general biology curriculum and in June 1976, graduated with a Bachelor of Arts degree. The following September she accepted a teaching assistantship through the Graduate Program in Ecology at The University of Tennessee, Knoxville and began study towards a Master of Science degree. That degree was conferred to her in June 1979.